

Review of the Papuan millipede genus *Acanthiulus* Gervais, 1844 (Diplopoda: Spirobolida: Pachybolidae)

urn:lsid:zoobank.org:pub:BE62AA7C-13C0-4256-9AD2-AD8098ED53B4

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Abstract: The genus *Acanthiulus*, which has hitherto been known to comprise three accepted species or subspecies endemic to the Papuan region, is revised, rediagnosed and shown to include only a single, quite variable species, *A. blainvillei* (Leguillou, 1841), with *A. blainvillei septemtrionalis* Attems, 1914 and *A. wollastoni* Hirst, 1914 both considered as its new subjective junior synonyms, syn. nov. Pronounced morphological variations, all clearly illustrated here, concern only peripheral characters, but the gonopodal structure remains very stable. Three morphs are distinguished: A, B and C. The distribution of *A. blainvillei* is mapped, the genus and species apparently being restricted to the Aru Archipelago, East Indonesia and much of New Guinea, both Indonesian and Papua New Guinea. Certain clinal variation patterns and an evolutionary scenario can be suggested in the distribution and polymorphism of the widespread species *A. blainvillei* at the northern periphery and in the centre of its distribution area.

Keywords: Millipede, taxonomy, new synonymy, iconography, polymorphism, microevolution, Papuan Region.

Introduction

According to the latest catalogue (Jeekel 2001), the Papuan genus *Acanthiulus* Gervais, 1844 is currently known to comprise only the following three accepted species or subspecies. These are *A. blainvillei* (Leguillou, 1841) (the type species of the genus, with several synonyms and a variety), from Indonesian, former Dutch New Guinea (Alkmaar, “Kajo Bay”, “between Njad and Sekopo” at Tami River, presently Papua Province of Indonesia), northern New Guinea, former Kaiser-Wilhelmsland, presently Papua New Guinea (Sepik River and Astrolabe Bay), and Aru Archipelago, East Indonesia (Dobo, Manoemai, Wokam, and Womar, East Indonesia); *A. blainvillei septemtrionalis* Attems, 1914, from western New Guinea (Tanah Merah Bay, Hollandia, coast south of Humboldt Bay, Bewani River, and Zoutbron near Begowri River, Papua, Indonesia); and *A. wollastoni* Hirst, 1914, from southwestern New Guinea (Mimika River, Papua, Indonesia).

Acanthiulus forms are very characteristic

due to most of the body rings/segments having a number of conspicuous cones or spines (Figs 1A, 1B). This is in stark contrast to the more commonly encountered, often large-sized and sympatric Spirobolida, which typically lack an ornamented integument. The generic etymology is based on this prominent ornamentation with “acantha” meaning “spine” in Greek.

Even though *Acanthiulus* is a small, oligotypic genus, its taxonomic history is quite convoluted (Jeekel 1971; 2001). It was first proposed as a subgenus of *Iulus* Linnaeus, 1758 (recte: *Julus*) by Gervais (1844) to encompass only *J. Blainvillii* (recte: *blainvillei*) Leguillou, 1841, from an unspecified locality in New Guinea. The species was briefly redescribed (Gervais 1844) and, a little later, schematically illustrated (Gervais 1847), apparently using the type material in the Paris Museum. The species was thereby erroneously transferred to the order Spirostreptida (Gervais 1847). Latzel (1884) suggested, but did not formalize the synonymy of *Acanthiulus* with *Trachyiulus* Peters, 1864 (recte: *Trachyjulus*), again a member of Spirostreptida,



while Bollman (1893) agreed to their close affinities, but rejected the synonymy.

Daday (1893) very imperfectly described and schematically illustrated a second species, *Spirobolus dentatus* Daday, 1893, from Kaiser-Wilhelmsland, New Guinea, which Silvestri (1895) synonymized with *Trigoniulus Blainvillii* [sic!], and provided its brief redescription. *Acanthiulus* was thus sunk under *Trigoniulus* Pocock, 1894, not vice versa.

Pocock (1893) was apparently the first to consider *Acanthiulus* as a genus of full rank in Spirobolida, close to *Spirobolus* Brandt, 1833, but easily distinguished by the presence of eight transverse rows of spines on most body rings. He also described a new species, *A. Murrayi* (recte: *murrayi*) Pocock, 1893, from “Wokan Dobbo”, Aru Islands, nicely illustrated the body sculpture, and corrected the spelling of the type species to *blainvillei*, albeit referred to it as *Blainvillei*.

Porat (1894) described another new species of *Acanthiulus*, this time from Cameroon, west-central Africa: *A. tuberculosus* Porat, 1894. In addition, he erected a new genus, *Thrinciulus* Porat, 1894, to accommodate two different new species from Cameroon, but designated *Acanthiulus murrayi* as its type species (cf. Carl (1913) and Jeekel (1971; 2001)). *Acanthiulus tuberculosus* has since Pocock (1903) been known to have nothing to do with the true *Acanthiulus*. Moreover, it has long become (even twice!) the type species of two formal genera of Spirostreptida, the valid one being *Tropiulus* Silvestri, 1896 (Jeekel 1971). Paradoxically, *Acanthiulus tuberculosus* is still listed as such on the web (<https://www.gbif.org/species/1026912>).

Bouvier (1903) described and beautifully illustrated yet another new species, *Acanthiulus maindroni* Bouvier, 1903, from southern India. However, like *A. tuberculosus*, it has nothing to do with the true *Acanthiulus*, albeit it does belong to the same family Pachybolidae, order Spirobolida. Bouvier (1903) also stated that he had examined the holotype of *Acanthiulus blainvillei* in the Paris Museum, and compared it to his *A. maindroni*. Brölemann (1903) provided a comparative study of the gonopods of *Acanthiulus* vis-à-vis several other genera of Spirobolida, for which, however, he used the gonopods of *maindroni*... At present, *maindroni* is considered as the sole accepted species of *Eucentrobolus* Pocock, 1903, a genus endemic to southern India (Golovatch & Wesener 2016).

Pocock (1903) must have overlooked Silvestri's (1895) proposed synonymy of Daday's *dentatus* with *blainvillei*, as well as Porat's (1894) earlier

typification of *Thrinciulus*. He was also so badly misled by Daday's (1893) erroneous statement that the ozopores in *dentatus* were located behind, not before the stricture on the body rings, that he created a new genus, *Polybunobolus* Pocock, 1903, for *murrayi* alone, as opposed to *blainvillei* and *dentatus* which remained in *Acanthiulus*. From the very start, *Polybunobolus* thus became an objective junior synonym of *Thrinciulus*.

Carl (1913) not only extensively discussed the taxonomy of *Acanthiulus*, but he also redescribed, nicely illustrated and recorded *A. murrayi* from three places in the Aru Islands: Teranhan: Ngaiguli; Wammer: Dobo; and Wokam: Samang. In addition, Carl (1913) formally synonymized *Polybunobolus* with *Acanthiulus*, but Brölemann (1913) questioned that synonymy and corrected the scope of *Acanthiulus* compared to his own earlier treatment (Brölemann 1903). He also provided a most detailed redescription and a number of line drawings of *A. blainvillei* coming from an unspecified locality in New Guinea; more importantly, he was the first to properly illustrate the gonopodal structure of *A. blainvillei* (reproduced here in Figs 29–32).

Attems (1914a) very concisely described a new subspecies and a variety of *A. blainvillei* from mainland New Guinea, i.e. *A. blainvillei* ssp. *septemtrionalis* Attems, 1914 and *A. blainvillei* var. *intermedius* Attems, 1914, also presenting a key to both subspecies and the variety of *A. blainvillei*. Chamberlin (1920) slightly misspelled the name *septemtrionalis* as *septentrionalis* [sic!] and, more importantly, once referred to the variety *intermedius* as *A. blainvillei intermedius*. However, as the latter name was clearly listed as a variety earlier in the same paper, it seems improper to formally treat *intermedius* as a subspecies and to allot it a taxonomic rank.

Finally, Hirst (1914) described a new species, *A. wollastoni* Hirst, 1914, from Dutch New Guinea (Mimika River), thus providing the latest contribution to the scope of *Acanthiulus*. As a result, Jeekel (2001) considered valid only the following three species or subspecies: *A. blainvillei* (Leguillou, 1841), *A. blainvillei septemtrionalis* Attems, 1914, and *A. wollastoni* Hirst, 1914.

Jeekel's (2001) catalogue of Indo-Pacific Spirobolida is fairly complete and relevant, but it makes sense to reiterate it in full at least as regards *Acanthiulus*, because it omitted a reference and some original spelling details of all species-level names.

The main objective of our contribution is to identify the *Acanthiulus* material housed in the



Zoological Museum of the Moscow University (ZMUM), Russia, as well as to present the first relevant iconography of *Acanthiulus*.

Material and methods

Most of the fresh samples were collected recently and donated to the ZMUM. All *Acanthiulus* material, both type and non-type, identified by Carl Attems and currently kept at the Natural History Museum of Vienna, Austria (NHMW) and the Naturalis Biodiversity Center, Leiden, The Netherlands (NBCL) has also been considered and properly illustrated. The type series of another congener housed in the Natural History Museum in London (BMNH) has also been accessed, revised and illustrated. On-spot field observations and images were made by one of us (DT) and Mārtiņš Kalniņš (Sigulda, Latvia). In addition, a specimen of *Acanthiulus* filmed at Bosavi Volcano, Papua New Guinea for BBC's "Lost land of the volcano" (<https://www.bbc.co.uk/programmes/b00m82h7>) has been identified from video and mapped as well.

Pictures were taken with a Canon EOS 5D digital camera and stacked using Zerene Stacker software (ZMUM), with a Nikon DS-Ri-2 camera mounted on a Nikon SMZ25 stereo microscope using NIS-Elements Microscope Imaging Software with an Extended Depth of Focus (EDF) patch (NHMW), a Nikon D800 with a Nikkor AF-S 105 mm Macro lens (RMNH), or a Zeiss Axio Zoom V.16 (BMNH).

Because numerous locality and even regional names in New Guinea have been notoriously changed or repeatedly misspelled, while some have simply vanished (e.g., Bronbeek, Modderlust or Tanah Merah Bay around Jayapura alone) over the island's historical record, an updated list of relevant toponyms is provided in the legend to Map. The modern name always follows earlier synonyms, if any.

In the catalogue sections per species below, D stands for a description or descriptive notes (sometimes also including a key, discussion, new status, synonymy or combination), R for new or old records, and M for mere mention.

Results

Family Pachybolidae

Genus *Acanthiulus* Gervais, 1844

Type species: *Julus Blainvillei* Leguillou, 1841,

by subsequent designation of Gervais (1844).

= *Thrinciulus* Porat, 1894

Type species: *Acanthiulus murrayi* Pocock, 1893, by subsequent designation of Porat (1894).

= *Polybunobolus* Pocock, 1903

Type species: *Acanthiulus murrayi* Pocock, 1893, by original designation.

A full generic synonymy list is available in Jeekel (2001). Because the genus appears to contain only one species, below we combine its diagnosis and description.

Diagnosis and description: A genus of particularly large-sized Pachybolidae (adults 100–210 mm long and 9–14.5 mm in diameter, and ♀♀ tend to be larger and bulkier than ♂♂) with the collum being smooth and bearing unusually prominent, relatively narrowly rounded, flap-shaped and sinuous paraterga drawn clearly below the venter, slightly more narrow in the ♂, distinctly bordered: narrowly along the anterior and lateral margins and especially broadly along the caudal margin (Figs 3, 9–10, 16, 19, 42, 62–65, 68). Most body rings are heavily sculptured and show a transverse row of 1+1, 3+3 or 4(5)+4(5) conspicuously enlarged cones or spines on each metazona, often with small intermediate crests, ribs, striae or bosses (Figs 1, 3–5, 9–12, 16–23, 33–36, 42–46, 52–56, 62–68, 71–72); the telson has a very small epiproct not overhanging the paraprocts and lacking a caudal process, each paraproct being distinctly impressed before the caudal marginal lip (Figs 5, 12, 22–23, 36, 46, 56, 63, 67, 72). The hypoproct is very wide and short, with an almost straight caudal margin. The adult body is with 50–55p+T segments/rings. The colouration is usually dark brown to blackish, rarely dark olivaceous, only the antennae and ozopores are sometimes contrasting red or yellowish (Figs 1, 3–5, 9–12, 16–23, 33–36, 42–46, 52–56, 62–68, 71–72), and the legs red-brown, occasionally with yellow tarsi. Eye patches round, ca 50 ommatidia arranged in eight vertical rows. Supralabral setae 2+2, the labrum has three distinct medial teeth inside a deep notch at, and a short, but evident axial suture/line above, the anterior margin (Figs 17, 18, 33, 43, 53, 65, 69). The antennae are short, C-shaped, a little longer and reaching the caudal margin of the collum in the ♂; antennomere 2 is the longest, antennomere 8 has four apical sensory cones (Figs 3, 9, 10, 16–19, 33, 42–43, 52–53, 62–65, 68–69). Striations on postcollum



rings are as usual: very fine, dense, vertical and often confused striations on prozonae; arcuate, somewhat more distinct, often similarly confused striations on mesozonae; and usually rough striae, also increasingly dense and distinct ventrad, on metazonae (Figs 3–5, 9–12, 16–23, 33–36, 42–46, 52–56, 62–68, 71–72). A pro-mesozonal line is absent. The tegument is mostly shining, delicately reticulate, in places micropunctate, only metazonae (but not their ornamentations!) are often rough and dull, sometimes coated with dirt. Scobinae absent, the limbus is unmodified. Ozopores starting with ring 6 and lying in the mesozona, well before the meso-metazonal suture/line (Figs 9, 10, 16, 19, 42, 52, 62–64, 68, 71–72). ♂ coxae are swollen ventrally, with one spine located above and 2–3 below the claw; all podomeres are more or less bulged ventrally, each of those lying proximal to the tarsus normally supports one seta. The penes are basally a single, but quickly and widely diverging structure, each branch consisting of 5–6 constricted rings and apically surmounted by a small papilla (Figs 17, 53). ♂ ring 7 is swollen ventrally, a complete ring bearing a clear ventral bridge in the caudal half (Figs 33, 44, 54, 70). ♂ legs are a little longer than ♀ ones, all ♂ coxae are rounded and somewhat swollen, prefemora and femora compressed laterally and slightly ridged ventrally, tarsi without sole pads (Figs 53–54). Both gonopod pairs mostly very heavily sclerotized. The anterior gonopods (Figs 6, 7, 13–15, 25–27, 29, 30, 37–38, 47–48, 57–58, 73–74) are with a broad sternite (s) attached laterobasally to tracheal apodemes (a) and extended medially into a high, distally bilobed, apically diverging and rounded central process (sp) which divides both coxae (cx) and consists of two medially fused halves still visibly separated by a deep suture. The coxae (cx) are set laterally on, and are only a little higher than, the sternal process (sp); each coxa (cx) is roundly subtriangular to squarish in shape, hollow on the caudal face and contains a smaller and similarly shaped telopodite (t) sunken inside the hollow; t is slightly bilobed apically, the more narrow, rounded and finger-shaped apical lobe lying mesally. The posterior gonopods (Figs 8, 28, 31–32, 39–41, 49–51, 59–61, 75–77) are 2-segmented, the sternite (s) being strongly chitinized, elongate, subcylindrical and transverse, divided, but fused centrally, either side with a small ampulla/vesicle and borne on a large tracheal apodeme (a). The coxa (cx) is rather simple, boat shaped, regularly and clearly curved mesad, mostly hollow on the mesal side; in the basal half it carries a seminal/

prostatic groove that originates from the ampulla and ends up at about cx midheight near a small, squarish, serrate and chitinized lobule (lo) at the bottom of the cx hollow. The apical part of cx is trifid, showing a larger, subapical and subtriangular lobe (lb), rounded to subacute, at the anterior margin, and two particularly small, apical denticles (d), both subacute to acute.

***Acanthiulus blainvillei* (Leguillou, 1841)** (Figs 1–77, map)

Julus Blainvillei [sic!] Leguillou, 1841: 279 (D).

Iulus Blainvillii [sic!] – Gervais 1844: 70 (D); 1847: 173 (D, pl.44, figs 8–8b).

Acanthiulus Blainvillii [sic!] – Preudhomme de Borre 1884: 52 (M).

Acanthiulus Blainvillei [sic!] – Preudhomme de Borre 1884: 63 (M); Pocock 1893: 137 (M); 1903: 531 (D); Bouvier 1903: 264 (M); Attems 1914b: 352 (M); 1915: 1, 6, 31 (D, figs 6–9); 1927: 62 (M).

Acanthiulus blainvillii [sic!] – Bollman 1893: 139 (M); Hoffman, Keeton 1960: 6 (M).

Spirobolus dentatus Daday, 1893: 101 (D, pl.3, figs 1–7), Wilhelmsland, New Guinea; synonymized by Silvestri (1895: 654); Carl 1913: 275, 276 (D); Jeekel 2001: 56 (M, R).

Acanthiulus Murrayi [sic!] Pocock 1893: 136 (D, pl.9, figs 7–7b), Wokan Dobbo, Aru Islands; synonymized by Attems (1914b: 351).

Acanthiulus dentatus – Pocock 1903: 531 (D); Carl 1913: 275, 276 (D).

Acanthiulus Murrayi [sic!] – Bouvier 1903: 264 (M); Attems 1914b: 352 (M).

Trigoniulus Blainvillii [sic!] – Silvestri 1895: 654 (D).

Polybunobolus Murrayi [sic!] – Pocock 1903: 531 (D).

Acanthiulus murrayi – Carl 1913: 276 (D, pl.11, figs 14–17), Aru Islands (Carl, 1913); Chamberlin 1920: 216 (M); Jeekel 2001: 56 (M, R).

Acanthiulus blainvillei – Brölemann 1913: 105, 109 (D, pl.15, figs 23–26), New Guinea, no precise locality; Attems 1914a: 383 (D); 1932: 4 (R, Manoembai, Aru Islands); Chamberlin 1920: 215 (M); Jeekel 1971: 191 (M); 2001: 55 (M, R).

Acanthiulus blainvillei var. *intermedius* Attems 1914a: 381, 382, 384 (D). Northern Dutch New Guinea: near Kajo Bay, between Njad and Sekopo at Tami River, and Astrolabe Bay (Attems, 1914a); Jeekel 2001: 56 (M, R).

Acanthiulus blainvillei var. *intermedius* – Chamberlin 1920: 215 (M); Moritz & Fischer 1975: 245 (M).

Acanthiulus blainvillei ssp. *septemtrionalis* Attems, 1914a: 383 (D), **syn. nov.** Northern Dutch New Guinea (Attems, 1914a); Jeekel 2001: 56 (M, R).

Acanthiulus Blainvillei [sic!] var. *intermedius* – Attems 1914b: 41, 84, 352 (M); 1915: 31 (M).

Acanthiulus Blainvillei [sic!] ssp. *septemtrionalis* Attems, 1914b: 41, 84, 352 (M); 1915: 32 (M).

Acanthiulus wollastoni Hirst, 1914: 330, fig. 17 (D), **syn.**



nov. Southern Dutch New Guinea (Hirst, 1914); Jeekel 2001: 56 (M, R).

Acanthiulus Blainvillei [sic!] – Attems 1915: 6, 7, 31 (D, figs 6–9). Southwestern (Alkmaar) and northern New Guinea (Kaiserin Augusta River), Aru Islands (Attems, 1915).

Acanthiulus blainvillei intermedius [sic!] – Chamberlin 1920: 267 (M).

Acanthiulus wollastoni – Chamberlin 1920: 216, 267 (M).

Type or original material: *Julus blainvillei*: ♀ holotype (Paris Museum, MNHN HB 008, J.-P. Mauriès & J.-J. Geoffroy *in litt.*; not examined); *Acanthiulus murrayi*: ♀ holotype (BMNH, not examined); *Spirobolus dentatus*:

♂ lectotype, ♂ paralectotype (Budapest Museum, HNHM 974.a.2/2, Korsós (1983) and *in litt.*; not examined); *Acanthiulus blainvillei* var. *intermedius* syntypes: 1 ♂ (NHMW 8433, Umgebung von Kajo Bai, zwischen Njad und Sekopo, P.N. van Kampen & K. Gjellerup leg. [Papua Province, Jayapura Regency, Muaralami District, between Nyao and Skouw seaside area], examined, Figs 3–8), 2 ♀♀ (NBCL RMNH DIP 562 and DIP 563, examined), 1 ♂, 3 ♀♀ (Berlin Museum, ZMB 5220–5222 (Moritz, 1975), not examined); *Acanthiulus blainvillei* ssp. *septemtrionalis* syntypes: 2 ♂♂, 5 ♀♀ (NBCL RMNH DIP 571–577, Indonesia, NE Papua, Tanah Merah Bay; Indonesia, NE Papua, Hollandia (= Jayapura, = Port Numbay), S2.538554, E140.705194; Indonesia, NE Papua, between biwak Kasawari and



Figures 1–2. Live ♂ (1A–B) and eggs (2) of *Acanthiulus blainvillei* (Leguillou, 1841), morph C, in the field from near Lake Kamakawalar, West Papua [not to scale] (image 2 courtesy Mārtiņš Kalniņš).



biwak Modderlust [S2.69, E140.85], = [Küstengebiet südlich von der Humboldtbai; Indonesia, NE Papua, Bewani River [am Bewani-Fluss]; Indonesia, NE Papua, between biwak Bronbeek and biwak Modderlust; Indonesia, NE Papua, biwak Zoutbron, 1910–1911, P.N. van Kampen & K. Gjellerup leg.; examined, Figs 9–15]; *Acanthiulus wollastoni* syntypes: 1 ♂, 1 ♀ (BMNH, British Ornithologists' Union Expedition and the Wollaston Expedition in Dutch New Guinea, Mimika River; examined, Figs 16–28); *Acanthiulus blainvillei*: 4 ♀♀ (NHMW 8432, Indonesia, Moluccas, Aru Islands, Kobroor Island, Manumbai, Trip Prince Leopold Belgium 1928/29, don. 1931, det. C. Attems; examined).

New material examined: *Acanthiulus blainvillei* (forma typica): 2 ♂♂, 3 ♀♀ (ZMUM), E Indonesia, West Papua Prov., S Bird's Neck Isthmus, 47 km E of Kaimana, Triton Bay, environs of Kamaka (former Warika) village, surroundings of Lake Kamakawalar, S3°46'22", E134°12'02", 60–310 m a.s.l., primary lowland tropical rainforest on limestone, 8.IX.2010, D. Telnov leg.; 1 ♂, 1 ♀ (ZMUM), same locality, S3°45'33", E134°12'05", 90 m a.s.l., primary lowland tropical rainforest on limestone, 8.IX.2010, M. Kalniņš leg.; 2 specimens (sex unknown), E Indonesia, West Papua Prov., S Bird's Neck Isthmus, 2–4 km NE of Kaimana, S3°39', E133°46', 150–200 m, 19–20.IX.2010, edge of disturbed lowland rainforest on limestone, leg. M. Kalniņš.

Acanthiulus blainvillei (forma *septemtrionalis*): 2 ♂♂, 1 ♀ (ZMUM), E Indonesia, West Papua Prov., 32 km SSE of Jayapura, near Indonesia – Papua New Guinea border cross point, S2°37'21", E140°58'42", 170–200 m a.s.l., primary lowland tropical rainforest on limestone, 17.III.2018; 1 ♂ (ZMUM), E Indonesia, Papua Prov., Star Mountains, 13.5 km SSE of Oksibil, S4°59'33", E140°42'02", 780 m a.s.l., primary lowland tropical rainforest, 14.III.2018.

Morphological variations and taxonomic implications

Numerous morphological characters of *Acanthiulus blainvillei* have been shown to vary, sometimes considerably so. The above diagnosis and description reflect most of the variable traits.

By far the most conspicuous variations concern tergal structures, in particular, the number and shape of metatergal teeth, cones or spines. Attems (1914a) was the first to recognise intraspecific categories within *A. blainvillei*, allocating them either to the rank of a subspecies (*septemtrionalis*) or a variety (*intermedius*) and paying special attention to that particular feature. His key to all three varieties can be repeated as follows (translated from German):

“1a. Each metazonite has 8 or 6 large and sometimes further smaller teeth, excluding metazonites 2 to 5

or 6, where rows gradually begin. All rows reach the penultimate segment. ♂, ♀ are with 50–52, mostly 51, body segments (New Guinea, Aru Islands) 2
2a. Large teeth on metazonites are long and sharp, and present in 8 rows. ♂ 9.6–11 mm wide
..... *blainvillei* Le Guillou.
2b. Large teeth on metazonites are much shorter and blunt, and present in 6 rows, the other rows are much smaller, sometimes totally absent. ♂ 13.5 mm, ♀ up to 14 mm wide var. *intermedius* Att.
1b. Each metazonite has only 2 large teeth, the rows begin from segment 6 or 7 and end on segment (3) 4 or 5 from behind. ♂, ♀ are with 53–56 body segments. Width 13.5–14.5 mm (northern Dutch New Guinea)
..... subsp. *septemtrionalis* n. subsp.”

In that key, Attems (1914a) unwillingly omitted *A. wollastoni* Hirst, 1914, because its description had not yet been published. Hirst (1914) characterized *A. wollastoni* as being blackish in colouration, with 50 body rings, and 103 (♂) or 115 mm (♀) in length and 9.1 (♂) or 10.2 mm (♀) in width. He compared *A. wollastoni* (two syntypes, ♂ and ♀) to *A. murrayi* (♀ holotype), stating that the antennomeres in *A. wollastoni* were stouter and enlarged distad (vs elongate and not so much enlarged in *A. murrayi*); the metaterga supported eight rows of “thorns”, of which four dorsal rows were much better developed than in *A. murrayi*, being obsolete or absent from rings 2 and 3, bosses on the 4th, spiniform from the 5th on, and all eight fully developed from the 7th. The caudal parts of the rings in *A. wollastoni* carried small ridges, and the paraprocts were less coarsely punctured posteriorly than in *A. murrayi*. Only the gonopods were illustrated (Figs 27–28). Having revised both syntypes of *A. wollastoni*, we take the opportunity to illustrate here most of its peripheral and gonopodal characters (Figs 16–23), with the exception of the posterior gonopod which was found either lost or misplaced.

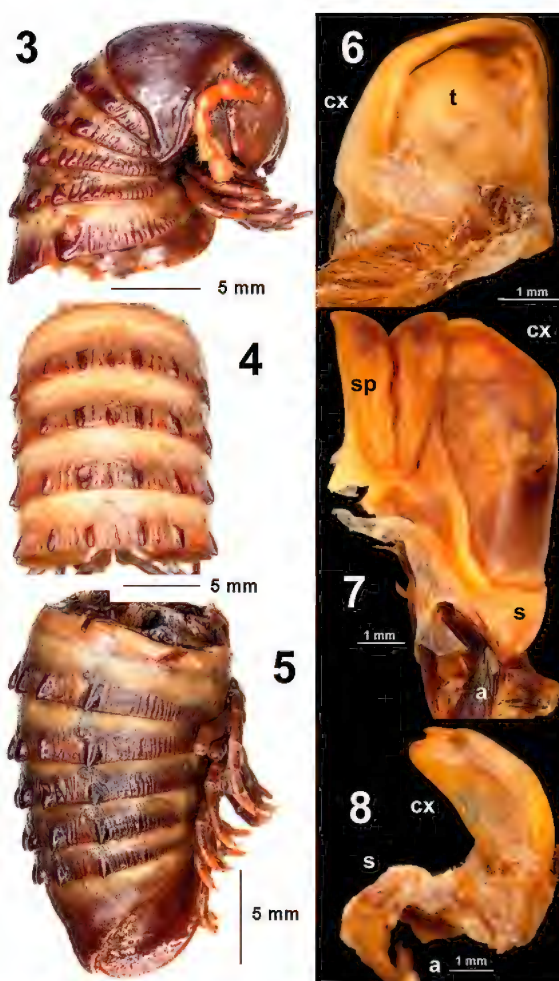
Given that *A. murrayi* has since Attems (1914b) been treated as a junior synonym of *A. blainvillei*, and that all of the characters of *A. wollastoni* fail to reflect more than individual variations observed in *A. blainvillei*, sometimes even sex-linked ones (e.g. the length of the antennae), we do not hesitate to formally consider *A. wollastoni* as another subjective junior synonym of *A. blainvillei*, **syn. nov.** In this connection, no lectotype designation is necessary for the type series of *A. wollastoni*.

The situation concerning the status of the subspecies *septemtrionalis* is not so straightforward, as the external differences between the typical form of *A. blainvillei* and the subspecies (= taxon) *septemtrionalis* are indeed very apparent (see



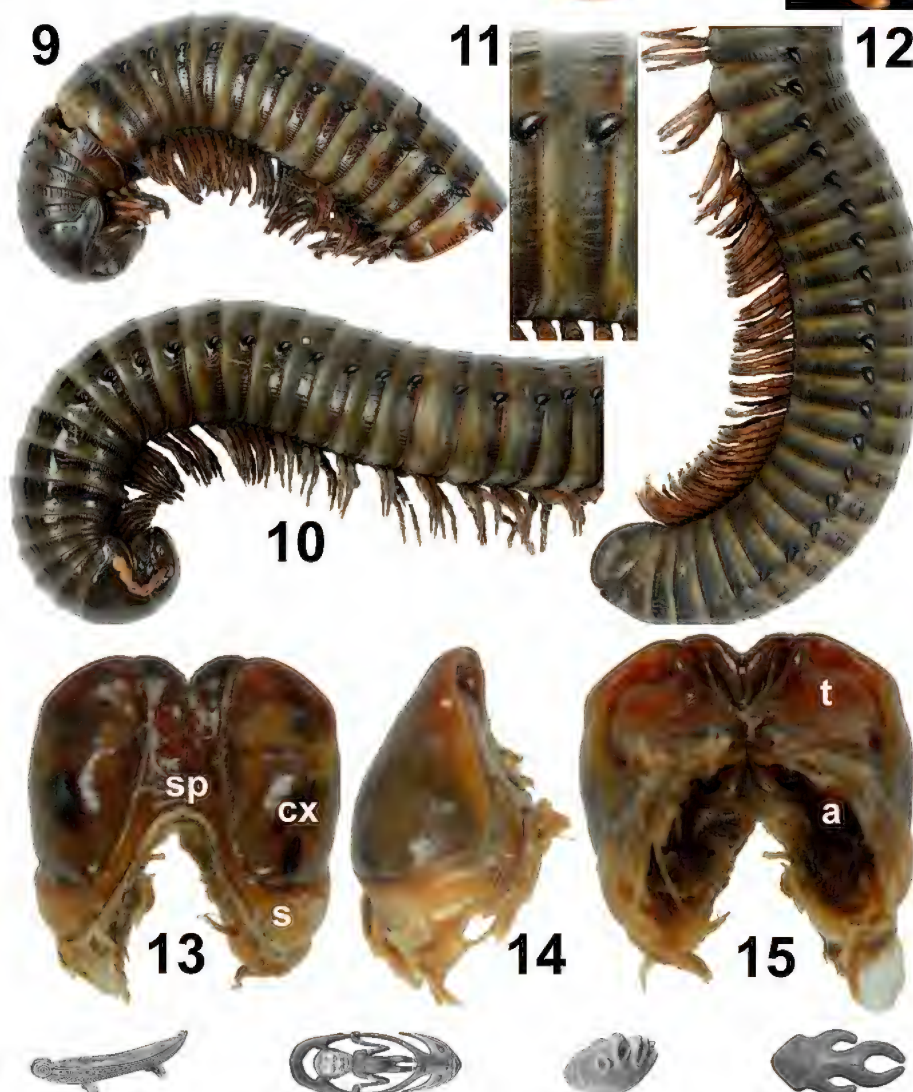
Figures 3–8. *Acanthiulus blainvillei* (Leguillou, 1841) ♂, morph B, from between Nyao and Skouw, NHMW 8433. 3 – Anterior part of body, lateral view; 4 – Midbody rings, dorsal view; 5 – Posterior part of body, lateral view; 6 – Left anterior gonopod, posterior view; 7 – Sternum and right anterior gonopod, anterior view; 8 – Left posterior gonopod, anterior view [not to scale] (images courtesy Oliver Macek).

Legends: a – Tracheal apodeme; cx – Coxa; s – Sternum; sp – Sternal process; t – Telopodite.



Figures 9–15. *Acanthiulus blainvillei* (Leguillou, 1841) ♂, morph A (♂♂ syntypes of *Acanthiulus blainvillei* ssp. *septemtrionalis* Attems, 1914), from Hollandia (= Jayapura, = Port Numbay), and between biwak Kasawari and biwak Modderlust, NBCL RMNH DIP 572 and DIP 573, respectively. 9–10 – Anterior parts of body, lateral views; 11 – Midbody rings, lateral view; 12 – Posterior part of body, lateral view; 13–15 – Anterior gonopods, anterior, lateral and posteroventral views, respectively [not to scale].

Legends: a – Tracheal apodeme; cx – Coxa; s – Sternum; sp – Sternal process; t – Telopodite.



the key above). However, given the features of the variety *intermedius* bridging those of *blainvillei* and *septemtrionalis*, we are inclined to follow Attems (1914a; 1914b) in treating *A. blainvillei* as a single, widespread and polymorphous species containing three morphological forms. Only the status of *septemtrionalis* is to be downgraded, and the following new formal synonymy advanced: *A. blainvillei septemtrionalis* is another subjective junior synonym of *A. blainvillei*, **syn. nov.** To avoid the use of Latin names for the infrasubspecific categories, and considering the least ornamented morph as evolutionarily basal, we designate *septemtrionalis* as morph A, *intermedius* as morph B, and the main form of *A. blainvillei* as morph C. No lectotype designation is likewise needed for the type series of *A. blainvillei septemtrionalis*. The same obviously concerns the series of syntypes of *A. intermedius*.

Variations in metatergal sculpture, primarily the size and shape of spines/teeth on the metazonae, are the best pronounced in morph C, apparently in relation to its particularly vast distribution and much more abundant material available for a comparative analysis. Cones start with ring 2 and on rings 6 or 7 they turn into *larger* spines/teeth that can be sharp and strongly inclined caudad, usually produced past the rear tergal margin, but sometimes they remain clearly shorter, blunt or rounded cones lying within the ring's hind contour. Each metazona has 8–10 strong spines, teeth or cones, these being less regular in the anterior half of the body and with some smaller intermediate ridges or denticles which are more conspicuous on rings 2–5(6). Spines invariably end on the last ring, just before the telson (Figs 22–23, 36, 46).

In morph B, obviously much more rare and localized, there are 3+3 strong, stout and mostly blunt or rounded cones, additionally also an axial and 2–4 much smaller, intermediate, longitudinal crests/ribs located between the larger, but still moderately strong teeth. Metatergal cones are evident and also start already with ring 2, quickly grow and turn into larger cones on all following rings (Figs 3–5). Attems (1914a) considered this variety as being more similar to morph C than to morph A.

Finally, morph A also seems to be rare and quite restricted in distribution. It shows only 1+1 strong cones/teeth on midbody metazonae, both located just below the ozopore level, with the bases of the teeth taking up most of the metazona length, and the tips acute or rounded and either drawn past or remaining within the caudal margin. Cones are traceable starting with ring 2, being

represented by rounded tubercles and gradually growing towards rings 6 to 9, to abruptly get fully or almost fully reduced only on the last few (usually three) rings before the telson. The dorsum between both lateral rows of teeth is roughly, longitudinally and irregularly rugose, with additional and usually barely traceable crests/ribs and/or denticles (Figs 9–12, 52–56, 62–68, 71–72).

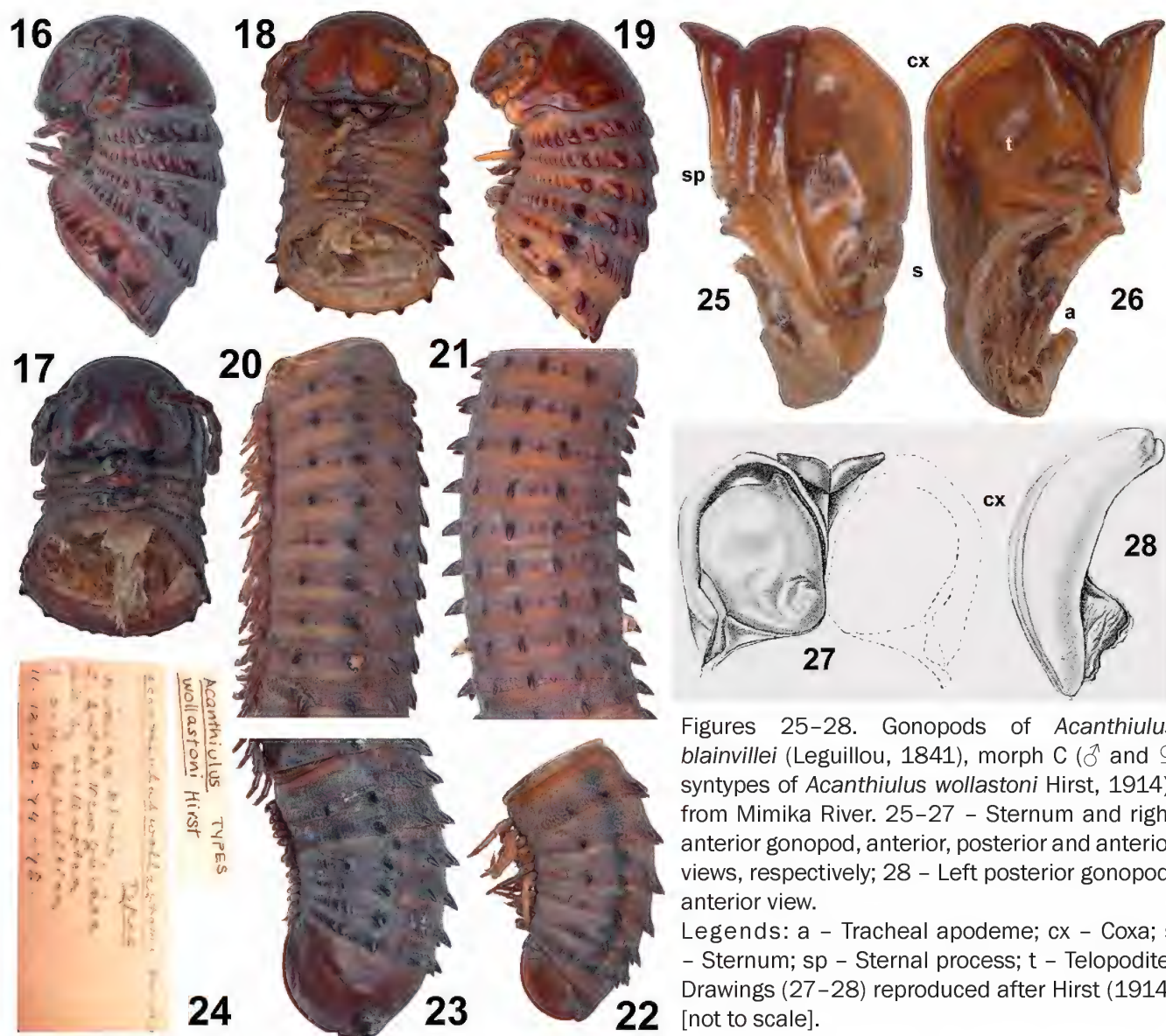
It seems that only because morph A is apparently more disjunct morphologically compared to both B and C that Attems (1914a), following the morphological subspecies concept, allotted it the rank of a subspecies. Instead we stick to the modern biological subspecies theory and practice (https://simple.wikipedia.org/wiki/Biological_species_concept), regarding A, B and C as morphs of a single polymorphous species.

As regards the number of body rings, it only seems to vary very little, 50–55p+T, since only adults seem to have hitherto been captured. Juvenile instars have still escaped from examination. This, against the background of very considerable size variations (10–21 cm long and 9–14.5 mm in diameter), clearly suggests several mature stadia in the development of *A. blainvillei*. As the entire order Spirobolida seems to grow with hemianamorphosis alone (Enghoff et al. 1993), it would be very interesting to trace the evolution of polymorphism in that remarkable species. Molecular studies seem very promising in this respect as well.

Among the main features that definitely remain very stable and prove to be most characteristic of the species as a whole, are the shape of a dorsally smooth collum, albeit with certain sex-linked variations, and the gonopodal structure (Figs 6–8, 13–15, 25–32, 37–41, 47–51, 57–61, 73–77). Morphological variation in the gonopodal conformation, the basic character accepted in modern diplopod systematics, appears to be so minor and virtually negligible that, following Attems (1914a), we tend to treat *A. blainvillei* as a remarkable, but typical example of infraspecific polymorphism, despite the often conspicuous peripheral differences between populations (morphs A, B and C). Another remarkable feature of *A. blainvillei* seems to be strict allopatry observed between the morphs (Map). The only exception superficially concerns *A. blainvillei* and *A. blainvillei intermedius*, both recorded from Kaiserin Augusta (= Sepik) River by Attems (1915), but no exact locality was presented for either form.

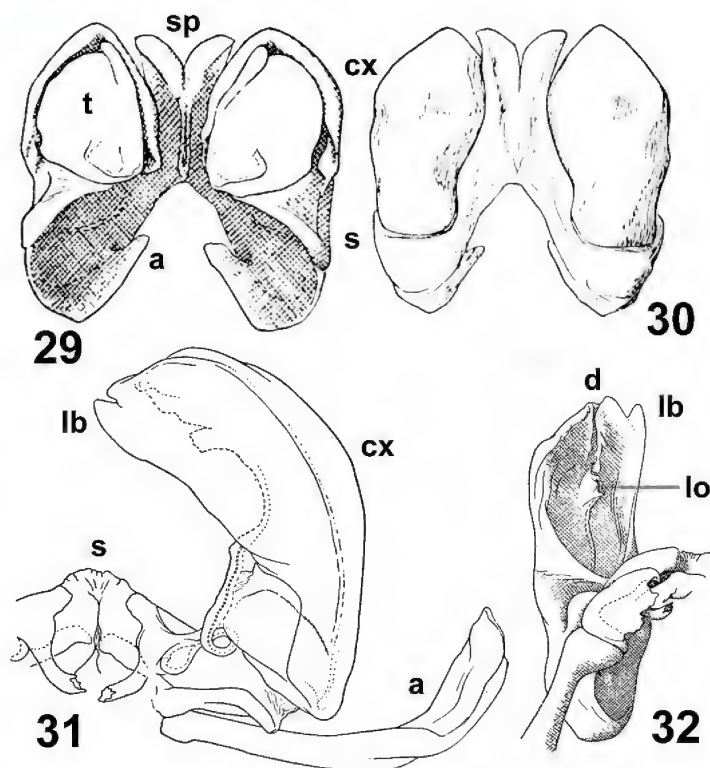
Moreover, the zone of pronounced polymorphism and microevolution appears to be relatively limited,

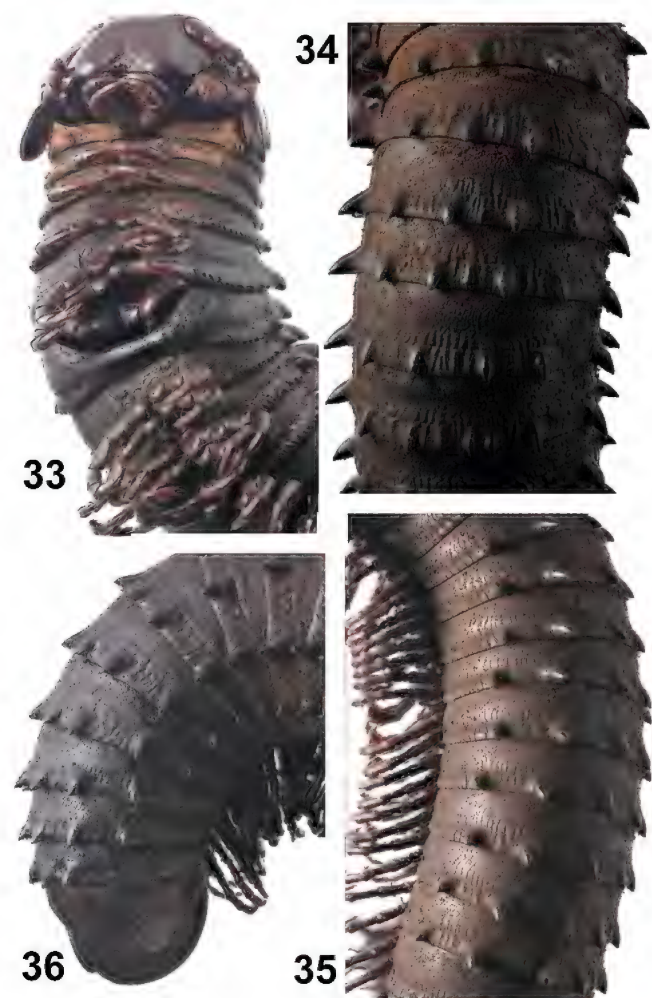




Figures 16-24. Original label (24), as well as ♂ (16-17 & 22) and ♀ (18-21 & 23) of *Acanthiulus blainvillei* (Leguillou, 1841), morph C (♂ and ♀ syntypes of *Acanthiulus wollastoni* Hirst, 1914), from Mimika River. 16-19 – Anterior parts of body, lateral, ventral, ventral and lateral views, respectively; 20-21 – Middle part of body, lateral and dorsal views, respectively; 22-23 – Posterior parts of body, lateral views [not to scale].

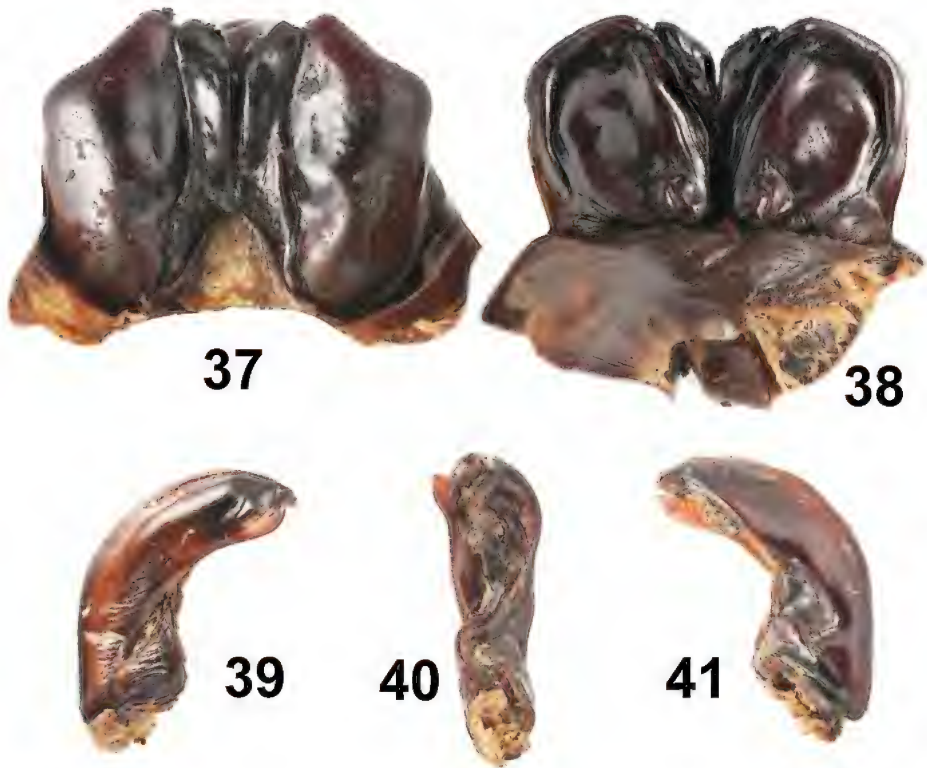
Figures 29-32. Gonopods of *Acanthiulus blainvillei* (Leguillou, 1841), morph C, ♂ from an unspecified locality in New Guinea. 29-30 – Both anterior gonopods, posterior and anterior views, respectively; 31-32 – Right posterior gonopod, anterior and mesal views, respectively. Legends: a – Tracheal apodeme; cx – Coxa; d – Two apical denticles; lb – Lobule at bottom of coxal hollow; lo – Subapical mesal lobe; s – Sternum; sp – Sternal process; t – Telopodite. Drawings reproduced after Brölemann (1913) [not to scale].





Figures 33–36. Habitus of *Acanthiulus blainvillei* (Leguillou, 1841), morph C, ♂ from near Lake Kamakawalar, West Papua. 33 – Anterior part of body, ventral view; 34–35 – Middle part of body, dorsal and lateral views, respectively; 36 – Posterior part of body, lateral view [not to scale] (images courtesy Kirill V. Makarov).

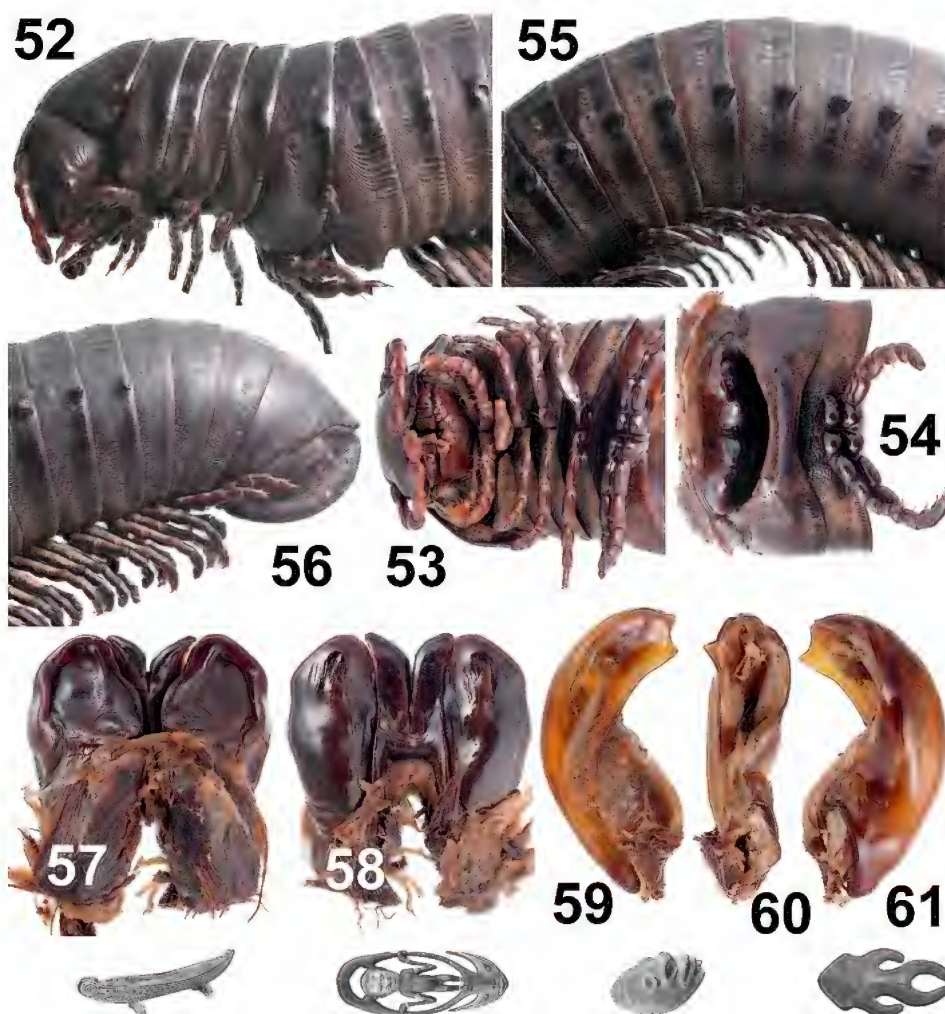
Figures 37–41. Gonopods of *Acanthiulus blainvillei* (Leguillou, 1841), morph C, ♂ from near Lake Kamakawalar. 37–38 – Both anterior gonopods, anterior and posterior views, respectively; 39–41 – Coxa of right posterior gonopod, anterior, mesal and posterior views, respectively [not to scale] (images courtesy Kirill V. Makarov).



Figures 42–51. *Acanthiulus blainvillei* (Leguillou, 1841), morph C, a different ♂ from near Lake Kamakawalar, West Papua. 42–43 – Anterior part of body, lateral and ventrocaudal views, respectively; 44 – Ring 7 with intact gonopods, ventral view; 45–46 – Middle and posterior parts of body, respectively, lateral views; 47–48 – Both anterior gonopods, anterior and posterior views, respectively; 49–51 – Coxa of right posterior gonopod, anterior, mesal and posterior views, respectively [not to scale] (images courtesy Kirill V. Makarov).



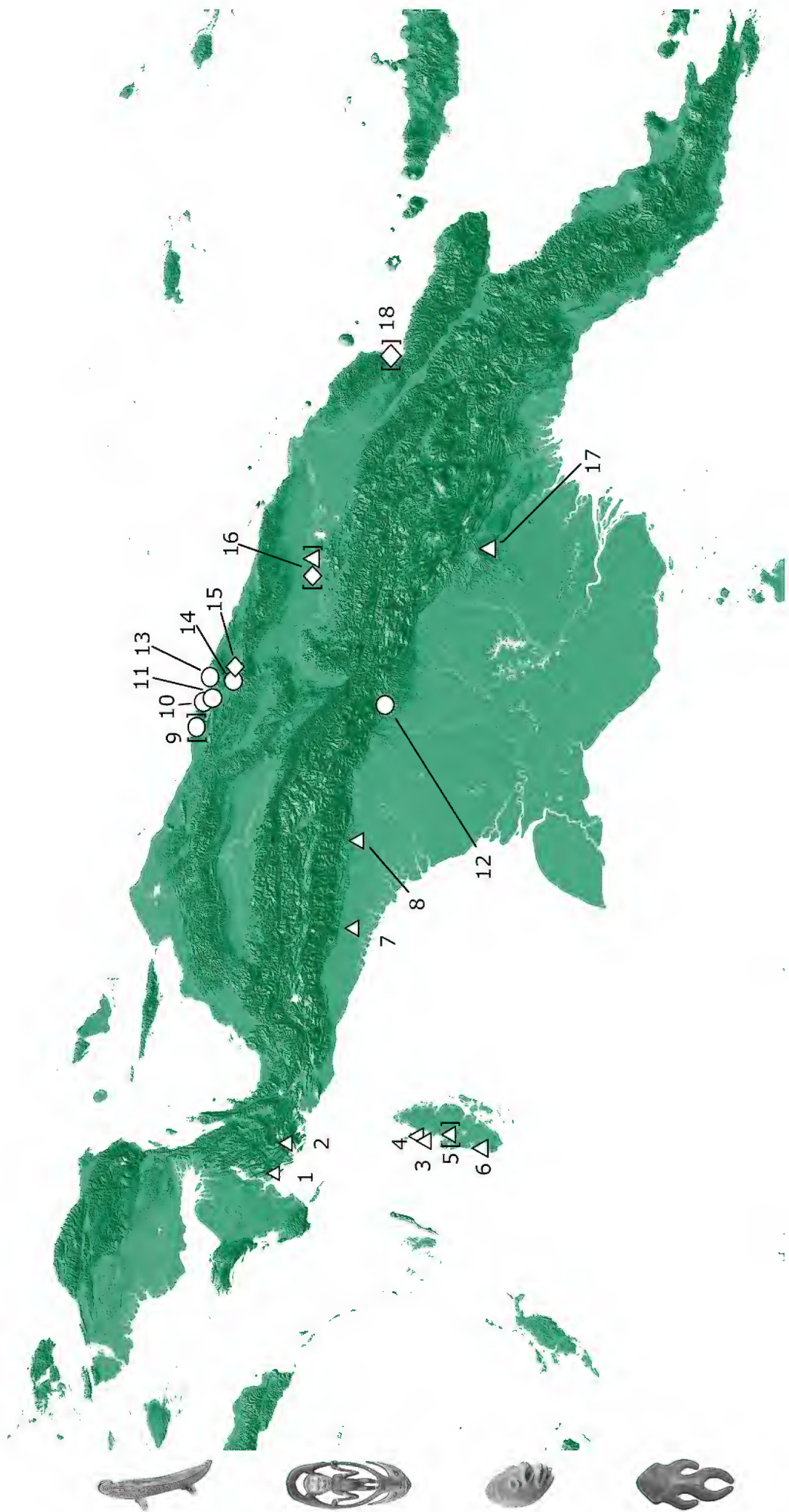
Figures 52–61. *Acanthiulus blainvillei* (Leguillou, 1841), morph A, ♂ from near Jayapura. 52–53 – Anterior part of body, lateral and ventral views, respectively (NB: left paratergum on collum broken off); 54 – Ring 7 with intact gonopods, ventral view; 55–56 – Middle and posterior parts of body, respectively, lateral views; 57–58 – Both anterior gonopods, posterior and anterior views, respectively; 59–61 – coxa of right posterior gonopod, anterior, mesal and posterior views, respectively. [not to scale] (images courtesy Kirill V. Makarov).





Figures 62–67. *Acanthiulus blainvillei* (Leguillou, 1841), morph A, ♂♂ from near Jayapura, Papua. 62 – Anterior part of body, lateral view (to show an intact right paratergum of collum); 63 – Habitus, lateral view; 64–65 – Anterior part of body, lateral and subventral views, respectively; 66–67 – Middle and posterior parts of body, respectively, lateral views [not to scale] (images courtesy Kirill V. Makarov).

Figures 68–77. *Acanthiulus blainvillei* (Leguillou, 1841), morph A, ♂ from near Oksibil. 68–69 – Anterior part of body, lateral and ventral views, respectively; 70 – Ring 7 with intact gonopods, ventral view; 71–72 – Middle and posterior parts of body, respectively, lateral views; 73–74 – Both anterior gonopods, anterior and posterior views, respectively; 75–77 – Coxa of right posterior gonopod, anterior, mesal and posterior views, respectively. [not to scale] (images courtesy Kirill V. Makarov).



being mainly restricted to northern and, to a lesser extent, central New Guinea (Map). If the presumably basalmost morph A indeed originated somewhere in that area, then the evolutionarily more advanced morph B and, especially, morph C could be viewed as later offshoots and expansion waves that have attained a still similarly restricted and a much wider distribution, respectively. The particularly successful and common morph C presently occurs over much of New Guinea and in the Aru Archipelago, but neither at the presumed origin centre near Jayapura nor in more or less central New Guinea (Map).

As an alternative viewpoint, superficially all or some of the morphs could also be regarded as independent species. For example, the particularly rare *A. intermedius* might be considered as a still somewhat underdeveloped *A. blainvillei*, i.e. its younger, but already fully mature ontogenetic stadium or stadia (Enghoff *et al.* 1993). However, this is hardly likely, because the ♂ and ♀ of *A. intermedius* attain the same, typically very large size (13.5 or 14 mm in diameter, respectively, and 51–52 body rings), while all three morphs, and this being especially important, share exactly the same gonopodal structure.

Notes on *Acanthiulus blainvillei* bionomy

The largest observed specimens of *Acanthiulus blainvillei* were the two females from northern New Guinea, from near the Indonesian – Papua New Guinean border crossing point (see above for locality details). Measured *in situ* (live specimens) by the fourth author: one female amounted to a total body length of 210 mm, while the second one to 190 mm. Unfortunately, that material was not preserved for subsequent laboratory study.

At all sites of the recent observations made in Indonesian New Guinea (the vicinities of Jayapura and Kaimana, Star Mountains, and Triton Bay, see above for details), *Acanthiulus* specimens were found in limestone-rich areas or immediately at the base of limestone rocks or hills. The presence of limestone in the habitat seems to be ecologically important if not crucial for this very large species which definitely requires a serious calcium supply to support its massive and hard exoskeleton.

The animals were observed feeding on fallen leaf litter, only partially decomposed (already brown) leaves being consumed by the millipedes. The population density of adults is very low, usually ca 2–3 specimens per 100–200 m² of primeval or secondary rainforest, as their active and purposeful

search on open ground and in various potential shelters like under logs and larger fallen leaves or in tree stumps shows. Juveniles are especially rarely encountered, since only a single young instar of ca 6 cm long was observed walking on the ground over the whole survey time (a few weeks in 2010 and 2018).

Oviposition in *A. blainvillei* was observed on the spot near the village of Warika, Bird's Neck Isthmus of New Guinea, by Mārtiņš Kalniņš and Dmitry Telnov. The female laid eggs separately, one by one, encapsulating each egg inside an ovoid “cocoon” ca 1–1.5 cm in diameter (Fig. 2). Each cocoon, or egg capsule was produced of excrement from an everted hind gut and, upon oviposition, it was flattened dorsoventrally on sides through tightly spiralling the body. The female left egg capsules directly on the rainforest ground.

Adult specimens taken in September 2010 survived for almost two years in captivity with neither breeding nor an oviposition success.

Acknowledgements

We are most grateful to Janet Beccaloni (BMNH), Oliver Macek (NHMW) and Kirill V. Makarov (Pedagogical State University, Moscow, Russia) for their help in arranging access to type material and taking some of the images for the present paper. Mārtiņš Kalniņš (Institute of Life Sciences and Technology, Daugavpils University, Latvia) is thanked for sharing specimens, observations, and images. Both Jean-Jacques Geoffroy and Jean-Paul Mauriès kindly provided information on the holotype of *Julus blainvillei* in the Paris Natural History Museum, while Zoltán Korsós on the types of *Spiroboldus dentatus* Daday, 1893 in the Budapest Natural History Museum.

Special thanks go to Jackson Means (Virginia Natural History Museum, Martinsville, U.S.A.) for his critical pre-review of an advanced draft.

The first author was supported by the Presidium of the Russian Academy of Sciences, Programme No 41 “Biodiversity of natural systems and biological resources of Russia”.

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Received: 21.xii.2020.

Accepted: 05.i.2021.



Appendix 1. Annotated list of localities.

An annotated locality list for morph A (circles): (7) “Mimika River”, Mimika Regency, Papua, Indonesia, about S4°30', E136°30'; no accurate data are available for this locality. (8) “Alkmaar”, nowadays a no longer extant camp of the First South New Guinea Expedition (1910), located at the place where the Lorentz River becomes unnavigable, Papua, Indonesia, about S4°40', E138°43'; no accurate data are available for this locality. (9) “Tanah Merah Bay”, west of Cyclops Mountains, Sentani-Jayapura area, Papua, Indonesia, about S2°27', E140°21'; no accurate data are available on this locality. (10) “Hollandia”, now Port Numbai in Jayapura, Papua, Indonesia, S2°32', E140°42'; this locality is now within the central Jayapura and does not exist. (11) comprises two published localities, “between biwak Bronbeek and biwak Modderlust” (about S2°39', E140°48' and S2°41', E140°50') and “between bivak Kasawari and bivak Modderlust” (about S2°37', E140°35' and S2°41', E140°50'), an area between the southern coast of Yotefa Bay towards Koya Timur and Tami River, Papua Indonesia; none of these three Dutch locality names is in use anymore and the area is mostly covered by settlements and rice fields, except few scattered still forested patches on limestone hills. (12) Star Mountains, 13.5 km SSE of Oksibil, Papua, Indonesia, S4°59'33", E140°42'02". (13) Jayapura 32 km SSE, near Indonesia – Papua New Guinea border crossing point, northeast of Bougainville Mountains, Papua, Indonesia, S2°37'21", E140°58'42". (14) comprises two published localities, “Bewani River” area and “bivak Zoutbron” (about S3°, E141° and S2°41', E140°59'), nowadays a no longer existing camp at Begowre River, south of Bougainville Mountains (on the Papua New Guinea border), Papua, Indonesia. (16) “Kaiserin-Augusta River”, now Sepik River, East Sepik Province, Papua New Guinea, about S4°12', E142°49'; the locality on the map is at the base camp of the “Kaiserin-Augusta-Fluß-Expedition” of 1912/13 since no accurate data are available for this locality.

An annotated locality list for morph B (diamonds): (15) “Umgebung von Kajo Bai, zwischen Njad und Sekopo” are misspelt Dutch locality names of Njao and Sekofro, in Sandaun (former West Sepik) Province, Papua New Guinea, south of Bougainville Mountains near the boundary with Indonesia, at the headwaters of one of the right hand side tributaries of Tami River, both nowadays uninhabited, about S2°40', E141°01'; this locality is about 8–10 km straight line from New Guinea's northern coast. (16) “Kaiserin-Augusta River”, now Sepik River, East Sepik Province, Papua New Guinea, about S4°12', E142°49'; the locality on the map is at the base camp of the “Kaiserin-Augusta-Fluß-Expedition” of 1912/13 since no accurate data are available for this locality. (18) “Astrolabe Bay”, Madang Province, Papua New Guinea, about S5°, E145°; no accurate data are available for this locality.

An annotated locality list for morph C (triangles): (1) S Bird's Neck Isthmus, 2–4 km NE of Kaimana, West Papua, Indonesia, S3°39', E133°46'. (2) Kaimana 47 km E, Triton Bay, environs of Kamaka (former Warika) village, surroundings of Lake Kamakawalar, West Papua, Indonesia, S3°46'22", E134°12'02". (3) “Wammer: Dobo”, Dobo, Wamar Island, Aru Islands, Indonesia, about S5°45', E134°13'. (4) “Wokam: Samang”, Samang District on SW peninsula of Wokam Island, Aru Islands, Indonesia, about S5°40', E134°14'. (5) “Manoemai, Wokam”, misspelling for Manoembai village on Manoembai River splitting Kobroor and Wokam, Aru Islands, about S6°01', E134°18'; no accurate data are available for this locality. (6) “Teranhan: Ngaiguli”, Ngaiguli, Trangan Island, Aru Islands, Indonesia, about S6°, E134°. (16) “Kaiserin-Augusta River”, now Sepik River, East Sepik Province, Papua New Guinea, about S4°12', E142°49'; the locality on the map is at the base camp of the “Kaiserin-Augusta-Fluß-Expedition” of 1912/13 since no accurate data are available for this locality. (17) Bosavi Volcano, Western Highlands Province, Papua New Guinea, about S6°43', E152°43'.

